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Social partners and temperature jointly affect morning foraging activity of small birds in winter

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Abstract

Daily foraging activity of small wintering birds is classically thought to be driven by the need to gather enough energy reserves to survive each night. A separate line of research has shown that sociality is a major driver in winter foraging activities in many species. Here, we used wintering birds as a study system to move toward an integrative understanding of the influence of energy requirements and sociality on foraging ecology. We used RFID-enabled feeders in Lincoln, Nebraska, USA in January–March 2019 to measure foraging activity in two species (downy woodpeckers, *Dryobates pubescens*, and white-breasted nuthatches, *Sitta carolinensis*). We analyzed the relationship between overnight temperature and morning foraging activity and found that lowest overnight temperature was weakly correlated with morning visitation at feeders. We then used a network approach to ask if flock associations explain similarity in birds' foraging activity. In both species, individuals with stronger associations in a social network were more likely to share similar

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feeder activity, and an index of social partners' activity explained foraging activity better than overnight temperature. This brings forth new questions about the interplay between individual response to temperature and social factors in shaping how small animals cope with harsh winter conditions.

Keywords: downy woodpecker, foraging flocks, RFID feeders, social networks, temperature, white-breasted nuthatch

Introduction

Winter is a period of low food availability and high thermal stress for animals living in temperate climates. For species that do not circumvent these challenges by way of migration or hibernation, energy budgets are tight and energy reserves must be replenished through frequent foraging bouts (Houston and McNamara 1993). While the need to maintain energy reserves during cold winters is not unique to birds, these challenges are particularly stark for small birds wintering in temperate climates because they must maintain relatively high body temperature within small bodies amidst low ambient temperatures (Grubb and Pravosudov 1994; Pravosudov and Lucas 2001; Heinrich 2003; Brodin 2007; Marchand 2013). Foraging strategies for these animals are classically hypothesized to reflect a tradeoff between starvation and predation risk (Lima 1986; Houston and McNamara 1993; McNamara et al. 1994). In these models, low temperatures increase overnight fat reserve requirements for small birds in winter when cold nightly temperatures deplete these reserves more quickly (Evans 1969; Bednekoff and Houston 1994; Broggi et al. 2007). However, maintaining larger fat reserves can come at the cost of increased predation risk because of increased time foraging (and reduced vigilance) or because fat reserves adversely affect agility (Blem 1975). Thus, small birds are expected to adjust their daily foraging efforts in various ways (e.g., overall foraging rate, diurnal foraging patterns, and patch selection) in response to winter temperature (Grubb 1978; Wachob 1996; McKnight 1998; Bonter et al. 2013).

In addition to energetic demands, social dynamics within foraging groups can influence activity patterns of winter resident animals. Group membership decreases individual predation risk (i.e., dilution; Hamilton 1971; Foster and Treherne 1981), reduces individual vigilance (i.e., "many eyes" hypothesis; Pulliam 1973; Krebs and Davies 1993),

and potentially increases foraging efficiency because animals spend less time scanning and more time foraging (Sullivan 1984; Vasquez and Kacelnik 2000; however, see Beauchamp 2005). Beyond simple effects of being in a group, there are additional social dynamics that can influence individual foraging patterns. For example, birds may benefit from foraging in a flock through socially learned information and behaviors (Aplin et al. 2012) and individual variation in foraging behavior can promote cohesion in between-patch flock movement (Aplin et al. 2014). Maintaining familiar flockmates may also minimize costs of group living by reducing the number of conflicts if familiar individuals are more tolerant of each other (Chaine et al. 2018). However, foraging in flocks can also come with costs, such as increased competition. For example, Ekman and Lilliendahl (1992) found that subordinate willow tits (*Parus montanus*) kept larger fat stores than dominants as extra insurance for restricted food access in times of low food availability. Furthermore, recent experiments have provided direct evidence that the activity patterns of social partners can affect individual foraging behaviors (Firth et al. 2015).

Energetic demands (and thus responses to temperature) and social dynamics both clearly influence foraging strategies of animals, but these two perspectives are rarely explored together. Our goal in this study was to assess how both the environment and social dynamics influence foraging patterns of small birds in winter. Our study focuses on two small, year-round woodland residents in North America: downy woodpeckers (*Dryobates pubescens*) and white-breasted nuthatches (*Sitta carolinensis*). These two species have been subject to studies of weather-dependent foraging strategies in winter (e.g., Grubb 1975, 1978). Both species maintain year-round territories, though their social behavior changes between breeding and nonbreeding seasons. For example, downy woodpeckers exhibit relatively loose social structure with little territorial defense and pair bonds during the winter (Matthysen 1993; Matthysen et al. 1993). Downy woodpeckers and white-breasted nuthatches both visit feeders in conspecific flocks, and they both also join mixed-species flocks as "satellite" species, following leader species such as blackcapped chickadees (*Poecile atricapillus)* and tufted titmice (*Baeolophus bicolor*; Berner and Grubb 1985). Thus, these species are well suited for this study, as they are exposed to both harsh winter conditions and their foraging activities are influenced by

multiple forms of social relations during foraging in winter.

Advances in data collection and analysis techniques (e.g., Radio frequency identification [RFID] data loggers and network analysis) have made it possible to investigate the dynamics of foraging activity and sociality in unprecedented detail. New RFID technology presents us with a powerful way to empirically test model predictions using activity data collected all day over many days, even on the coldest days of winter (e.g., Bonter et al. 2013; Moiron et al. 2018; Pitera et al. 2018). Furthermore, fine-scale feeder visitation data can be used to infer the composition of foraging flocks based on which birds were detected at feeders close together in time (Psorakis et al. 2012), and this flock composition data can be used to construct social networks (Farine 2013). Here, we leverage these approaches to explore the interplay between energetic demands and social dynamics on foraging activities of winter resident birds in the temperate zone.

In this study, we considered both environmental and social influences on foraging activity of small birds in winter. First, we considered the effect of lowest overnight temperature (hereafter, overnight temperature) on individual feeder visitation activity during the following morning because after especially cold nights energy stores would be depleted and birds would need to forage at higher rates (Bednekoff and Houston 1994). We then examined the relationship between individual variation in feeder visitation rates and sociality by asking whether pairs of birds that were more connected in the social network (i.e., flocked together more often) changed their foraging activity in similar ways across days. Finally, we tested the joint effects of environment and social factors by modeling the effects of both overnight temperature and activity patterns of social partners on individual activity patterns. These analyses do not fully decouple the potential influence of temperature and sociality—that is, because all individuals in a natural population are exposed to the same overall temperature fluctuations, the activity of one's social partners also reflect the effect of temperature on each individual. However, we propose further experimental approaches that can lead us to a better understanding of how social and physiological factors contribute to the foraging ecology of birds in thermally challenging environments.

Methods

Study site

We conducted our study from 26 January 2019 to 1 March 2019 at the Pioneers Park Nature Center (PPNC) in Lincoln, Nebraska, USA. The study site includes a small deciduous forest interwoven with dredged wetlands and gardens. PPNC is a public recreation area and is exposed to moderate foot traffic by visitors and park staff. Lincoln experiences a wide breadth of yearly temperatures (−12 to 32 °C) and annual precipitation is between 64 and 91 cm (Schneider et al. 2011). Lowest overnight temperatures ranged from −22 to 4 °C during the study period.

Data collection

We caught birds using mist nets near bird feeders at PPNC. We banded all captured birds with aluminum leg bands distributed by the United States Fish and Wildlife Services (USFWS) and we placed RFID leg bands (Eccel Technology, Leicester UK) on downy woodpeckers (n = 18) and white-breasted nuthatches (n = 13). Before release, we also collected morphological metrics including weight, culmen, tarsus, and wing length. Individuals were sexed by plumage.

We distributed eight RFID feeders of uniform design over an area of approximately 150,866 m^2, with a mean distance of approximately 287 m between feeders (**Figure** 1a). Feeders were hung from trees using a rope and pulley system, and we chose locations to avoid placing feeders close to low hanging branches, thereby preventing squirrels from damaging equipment or displacing birds at the feeders. The feeders were spaced as evenly as possible (i.e., given availability of suitable trees) to maximize coverage of the field site. Each feeder (New Generation(R) 23 inch feeder: Droll Yankee, Plainfield, CT) was equipped with an IBT EM4102 data logger board (Eccel Technology, Leicester, UK) to record RFID tag, date, and time when a bird visited the feeder. Each data logger was kept inside a sealed plastic container attached underneath the feeder (Figure 1b). Antennas were attached to a wooden platform attached to the bottom of the feeder so that birds

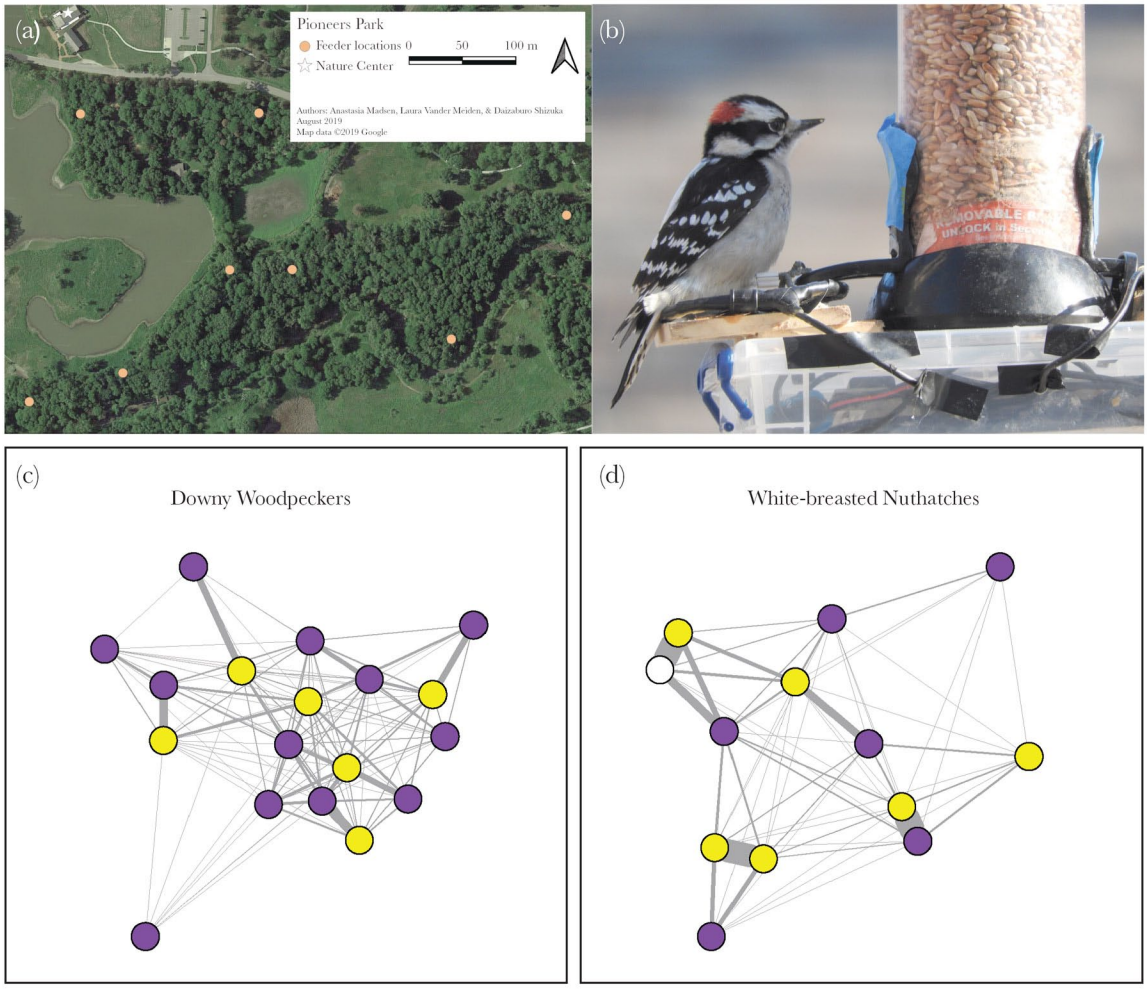

Figure 1 Study design showing the (a) distribution of feeders at the study site in Lincoln, Nebraska, USA, (b) RFID feeder setup (photographed with a tagged downy woodpecker), (c) downy woodpecker social network, and (d) white-breasted nuthatch social network. Network figures represent each individual as nodes (purple = male, yellow = female), connected by edges whose widths are proportional to the association index calculated from group associations detected at feeders.

would perch on them while accessing one of the bottom two openings of the feeder (Figure 1b). The other four openings were blocked with cork to prevent seed access. Data loggers were programmed to scan for RFID tags every . second from 6:30 AM to 8:00 PM. We checked feeders every 2–3 days to change batteries, download data, refill seed, and perform necessary maintenance. We filled all feeders with non-germinating safflower seed.

We collected weather data from the Lincoln Municipal Airport (approximately 8.4 km from the study site) weather station through the Weather Underground website (https://www.wunderground.com/history , accessed 11 April 2019). While we were not able to measure the temperature directly within our field site during data collection, data from a weather station deployed after our study (21 March 2019 to 9 April 2019) show that the temperature at the two sites are tightly correlated (Supplementary Materials).

Data analysis

We used feeder data from mornings (all records 6:30 AM to noon each day) on 26 January 2019 to 9 March 2019 for our final analysis. We focused on morning visitations in order to measure the immediate effects of overnight temperature on feeding activity. Data from 24–25 January 2019 and 10–17 March 2019 were removed because only a portion of the feeders were deployed for these periods due to staggered deployment and removal for repairs. All data processing and analyses were completed using the R statistical environment (R Development Team 2019). Because we observed that the feeders could detect birds more than once during a single visit, we condensed these data into discrete visits using an empirical cumulative distribution function (similar to Crates et al. 2016; Milligan et al. 2017). After 2 s, the density distribution of time delays exponentially decreased and we found it reasonable to accept that any detection of the same bird within 2 s was likely to be part of the same feeder visit (Supplementary Methods). For a given bird, we collapsed consecutive detections ≤ 2 s apart into a single visit at the time of the first detection (Supplementary Figure S2).

Construction and analysis of social networks

To measure patterns of social associations between individuals, we built a social network representing rates of associations between individuals in foraging flocks using data from all visits during the day (i.e., we did not restrict association data to mornings). We used a Gaussian Mixture Model, which uses machine learning algorithms to identify gathering events (Psorakis et al. 2012, 2015; implemented using the R

package *asnipe*, Farine 2013, Supplementary Materials). This method has been used to infer flock membership and association patterns in birds with similar ecology (e.g., Voelkl et al. 2016; Evans and Morand-Ferron 2019). All birds detected during the same gathering events were considered to be in the same foraging flock. Using these defined flocks, we constructed an adjacency matrix for each species using the Simple Ratio Index (SRI: Cairns and Schwager 1987) as edge weights. Cairns and Schwager (1987) identified SRI as the most appropriate association index when there is no bias in detecting individuals in groups or alone, as was the case here.

For each species, we measured two aspects of social structure: *social differentiation* and *assortment by sex*. Social differentiation is measured as the coefficient of variation (CV) of association indices (Whitehead 2008), and this describes the degree to which there are different types of social relationships within the population. High levels of social differentiation (i.e., high CV of association indices) indicates that some pairs maintain close associations (e.g., pair bonds) while others maintain loose, infrequent associations (e.g., casual flockmates). Low levels of social differentiation (i.e., low CV) indicate that all pairs of individuals associate with others equally. To test whether observed levels of social differentiation were different than expected from a null model, we compared the empirical CV of association indices against the CV of association indices in 1000 randomized networks which were constructed by swapping group membership within days using *asnipe* (Farine 2013). We conducted group membership swaps within days to preserve variation in how individual foraging rates change across days (i.e., the main variable of interest in our analyses).

Second, we assessed how the sex of individuals affected patterns of social connections. We measured the assortment coefficient (Newman 2002; Farine 2014) by sex for each network. If breeding pairs associate strongly with each other (as expected based on prior results: Matthysen 1993), we expect negative assortment by sex (i.e., males are more likely to associate with females and vice versa), though some of this pattern may be diluted by the social connections of juveniles. To test whether the observed level of assortment by sex was different than expected, we compared the empirical assortment coefficient against the assortment in 1000 networks in which the sex of individual was randomized (node-label permutation). We used the *assortnet* package (Farine 2014) in R to measure the assortment coefficient.

Effect of overnight temperature on foraging activity

To investigate the relationship between overnight temperature and morning visitation rates, we used two different modeling approaches. First, we used generalized linear mixed models (GLMMs) with the R package lme4 to investigate relationships between temperature and feeder visitation. In the GLMM analysis, the dependent variable was the number of feeder visitations (to any feeder) by an individual in a given morning, the fixed effect was the minimum temperature during the previous night, and the random effects were the individual RFID and the feeder location. Next, we used generalized additive mixed models (GAMMs) in the R package *mgcv* (R Development Team 2019) to visualize nonlinear patterns of the relationship between temperature and feeder visitation. As in the GLMM analysis, the dependent variable was the number of feeder visitations (to any feeder) by an individual in a given morning, the fixed effect was the minimum temperature during the previous night, and the random effects were the individual RFID and the feeder location. For both model types, we built separate models for each species and specified a log-link function to account for Poisson-distributed data.

Effect of social network on similarity in foraging activity

To investigate how foraging activities may be influenced by activities of flockmates, we used a matrix regression approach to compare pairwise similarities in morning foraging activity with social associations. First, we built a matrix to represent pairwise similarity of foraging activity between individuals. For each individual, we calculated z-scores of foraging rate to normalize data for comparison using the equation

$$z_i = \frac{x_i - \bar{x}}{\sigma_x}$$

where x_i was the number of visits by an individual on day i, x represented the mean morning visits for all days of the season, and σ_x was the standard deviation of x. We then generated a correlation matrix of these z-scores using the *simil* function (R package *proxy*), which represented the *activity similarity matrix*. Pairs of individuals that were more correlated in their profiles of morning foraging rate were

more synchronized in how they changed morning foraging activities across days.

Finally, to account for potential effects of spatial overlap on observed activity patterns, we built a *feeder overlap matrix* representing pairwise similarity in proportion of visits to each feeder location. For each individual, we calculated the number of times they visited each feeder over the course of the study, then divided this number by the total number of visits to get the proportion of visits to each feeder. We then calculated the pairwise correlation coefficients between each pair of individuals for the relative proportions of time spent at each feeder.

We used a multiple regression quadratic assignment procedure (MRQAP) to test whether the activity similarity matrix is explained by (i) social network (adjacency matrix) while accounting for (ii) spatial overlap (feeder overlap matrix). Two-tailed *P*-values were generated by the Double Semi-Partialling method (Dekker 2007) in *asnipe* (Farine 2013). We normalized values of each matrix to values between 0 and 1 prior to running the MRQAP analysis to facilitate comparisons between the observed effects and expected effects based on null model networks generated by group membership swaps (Farine 2013; Supplemental Methods). This normalization is necessary because group permutation methods used for the null model approach generate edge weights with very different means and variances than the observed social network. Specifically, we used the *asnipe* package (Farine 2013) to implement group membership swaps within days to create randomized networks that preserved variation in how individual foraging rates change across days (i.e., the main variable of interest in our analyses). Further details of our null model approach are presented in the Supplemental Materials.

Joint effects of temperature and social factors on foraging activity

Finally, we modeled the joint effects of temperature and social influence on morning foraging activity. We constructed linear mixed-models (LMM) with the z-scores of the morning foraging activity as the dependent variable and individual ID as the random effect. The fixed effects were the overnight temperature, morning activity patterns of

flockmates, and their interaction. The activity patterns of flockmates, S_i, for a given focal individual, *i,* was captured by:

$$S_i = \sum_{j \neq I} z_j \frac{A_{ij}}{k_i}$$

where A_{ij} is the association index between individual *i* and individual *j*, k_i is the total sum of edge weights connected to individual *i*, and Z_j is the z-score of morning foraging activity of individual *j*. Thus, this index sums the activity patterns of social partners of individual *i*, weighed by their relative strengths of association with *i*. Note that this analysis differs slightly from the GLMM analysis of overnight temperature (which uses the number of morning feeder visits per day as dependent variable) by using z-scores to yield standardized measurements of daily changes in foraging activity between the focal individual and its social partners.

We have provided code scripts for all analyses in Supplemental Materials.

Results

Description of the winter social networks

In both species, all individuals were connected in a single social network (Figure 1c,d). Both species were characterized by high social differentiation compared to random (downy woodpeckers: observed CV of association index = 1.28, expected CV from randomized networks = 0.66–0.73 (95% CI), $P < 0.001$; white-breasted nuthatches: observed CV of association index = 2.18, expected CV from randomized networks = 0.82–0.90 (95% CI), $P < 0.001$). This indicates that some pairs maintained close associations while other pair-wise associations were fleeting. Furthermore, the social network was negatively assorted by sex, indicating that male–female associations were relatively stronger than intrasexual associations, though this was not statistically significant for white-breasted nuthatches (downy woodpeckers: observed assortment coefficient = −0.34, expected assortment from randomized sex = −0.29 to 0.13 (95% CI), $P = 0.008$; whitebreasted nuthatches: observed assortment coefficient = −0.30, expected assortment from randomized sex = −0.54 to 0.27 (95% CI), $P = 0.23$). In

summary, the winter social structure of both species is characterized by a combination of some strong male–female relations (likely mating pairs) and other associations between conspecific flockmates.

Effect of overnight temperature on foraging activity

Overnight temperature fluctuated between −22.2 °C and 3.9 °C during the study period. GLMMs showed a weak, though statistically significant, negative relationship between morning feeder visitation and overnight temperature for downy woodpeckers ($P < 0.001$, estimate = −0.12, standard error = 0.007, $z = -16.4$, marginal $R^2 = 0.06$, conditional $R^2 = 0.88$) and white-breasted nuthatches ($P < 0.001$, estimate = −0.06, standard error = 0.01, $z = -5.8$, marginal $R^2 = 0.008$, conditional $R^2 = 0.92$). Visualization of the relationship using GAMM shows that, overall, feeder visitation of downy woodpeckers showed a clearer response to variation in overnight temperature than that of white-breasted nuthatches (**Figure 2**). However, overnight temperature alone explained a relatively small amount of variation in feeder visitation rates in both species.

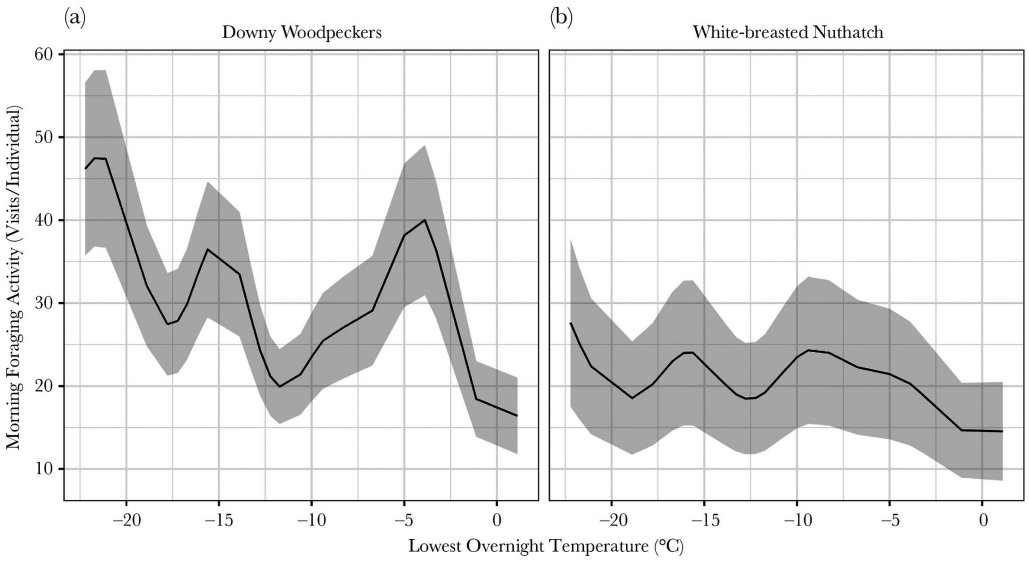

Figure 2 Predicted morning foraging activity (6:30 AM to noon) at RFID feeders over a range of overnight temperatures experienced from 26 January 2019 to 9 March 2019 in Lincoln, Nebraska, USA for (a) downy woodpeckers and (b) white-breasted nuthatches. Predicted values and standard error bands were calculated from log-link GAMMs fitted with thin plate regression splines in package *mgcv* (R Development Team 2019).

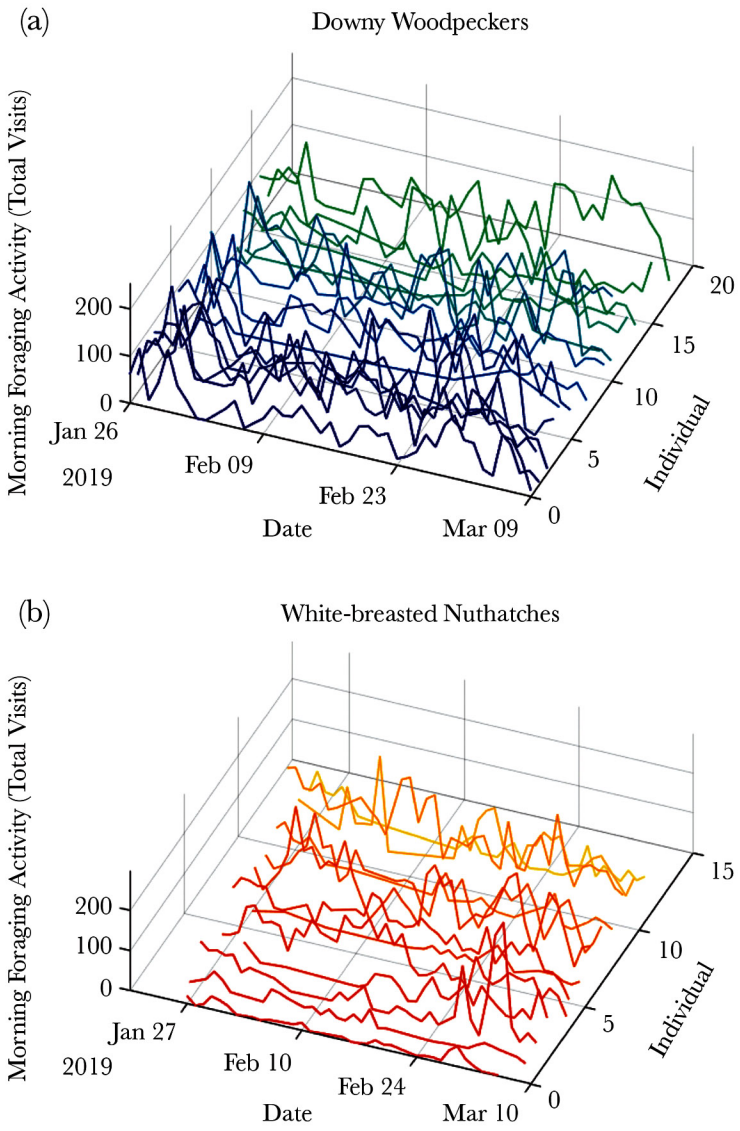

Figure 3 Individual daily feeder visitation profiles in Lincoln, NE, USA for **(a)** downy woodpeckers and **(b)** white-breasted nuthatches. Profiles reflect individuals' summed morning feeder visitations per day over the extent of the study period (26 January 2019 to 9 March 2019). Lines are colored to help visually separate individual profiles.

The poor fit between overnight temperature and morning visitation rates was in part due to high levels of variation in individual profiles of morning feeder visitations (captured by the difference between marginal and conditional R^2 values, which represent the fit of the model excluding and including random effects, respectively; visualized in **Figure 3**). In both species, some individuals predictably increased

morning feeder visitation with colder overnight temperature, while others showed no such response (Supplementary Figures S3 and S4). Given these results, we next sought to ask whether the individual variation in this morning feeder visitation profiles could be explained by the effects of social foraging.

Effect of social network on similarity in foraging activity

For both species, pairwise similarities in feeder visitation profiles between individuals were significantly predicted by their association index in the social network, but not by the similarity in which feeders they use (**Table 1**; downy woodpecker: effect of association = 0.45 effect of feeder overlap = −0.02; white-breasted nuthatch: effect of association = 0.48, effect of feeder overlap = 0.09). Thus, birds that were more strongly connected in the social network changed their morning feeder visitation rates in similar ways. Null model analysis confirmed the significant effects of the social network on morning foraging activity in both species: the estimate of the effect of the observed association index on similarity of feeder visitation profiles was greater than that expected from a null model in which group associations were randomized (downy woodpecker: observed effect = 0.46, effect estimated from null model = 0.03–0.07 (95% CI), $P < 0.001$; white-breasted nuthatch: observed effect = 0.47, effect estimated from null model = −0.02 to 0.01 (95% CI), $P < 0.001$).

Table 1 MRQAPs were used to compare the dependent matrix, a matrix representing similarity in foraging activity, with two independent matrices, an adjacency matrix and a matrix representing similarity in proportion of time spent at each feeder (package *asnipe,* R Development Team 2019). We calculated separate MRQAPs for downy woodpeckers (*Dryobates pubescens*) and white-breasted nuthatches (*Sitta carolinensis*). All matrices were normalized to values between 0 and 1 prior to the MRQAP analysis (see Supplementary Materials).

Downy woodpeckers			*White-breasted nuthatches*		
Independent variable	*Estimate*	*Two-tailed P-value*	*Independent variable*	*Estimate*	*Two-tailed P-value*
Intercept	0.50	<0.001	Intercept	0.38	<0.001
Adjacency matrix	0.45	<0.001	Adjacency matrix	0.48	0.001
Feeder overlap matrix	−0.02	0.88	Feeder overlap matrix	0.09	0.37
Adjusted R^2 = 0.14, residual SE = 0.18, df = 150			Adjusted R^2 = 0.36, residual SE = 0.14, df = 75		

Table 2 Linear Mixed Model analysis testing the effects of overnight temperature and social partner activity on the morning feeder visitation of individual downy woodpeckers (*Dryobates pubescens*) and white-breasted nuthatches (*Sitta carolinensis*).

Downy woodpeckers			*White-breasted nuthatches*		
Independent variable	*t-value*	*P-value*	*Independent variable*	*t-value*	*P-value*
Intercept	−5.41	<0.001	Intercept	−4.47	<0.001
Overnight temperature	−1.95	0.05	Overnight temperature	−0.90	0.37
Social partners	13.59	<0.001	Social partners	15.65	<0.001
Overnight temperature × Social partners	−0.03	0.97	Overnight temperature × Social partners	1.44	0.15
Marginal R^2 = 0.27, Conditional R^2 = 0.27			Marginal R^2 = 0.34, Conditional R^2 = 0.36		

Joint effects of temperature and social factors on foraging activity

Finally, we assessed how overnight temperature and the activity of an individual's social partners may jointly affect the morning feeder visitation rates of individuals by including both effects in the same model. For both species, our index of the activity patterns of an individual's social partners was a strong predictor of morning feeder visitation rates, but overnight temperature was not (**Table 2**; downy woodpeckers: effect of overnight temperature (t-value) = −1.95, P = 0.05; effect of social partners' activity (t-value) = 13.6, P < 0.001; white-breasted nuthatches: effect of overnight temperature (t-value) = −0.90, P = 0.37; effect of social partners' activity (t-value) = 15.6, P < 0.001). We note that the activity patterns of all individual birds could be affected by temperature at the same time, and our measure of activity of social partners includes this effect. Thus, this analysis does not isolate the effects of temperature *versus* social effects. Most likely, both factors play a role in affecting an individual's foraging activity, and this is captured in our metric of social partners' activity.

Discussion

We examined how overnight temperature and activity patterns of social partners affected feeder visitation rates of small birds in winter. We found that foraging activity was significantly but weakly correlated with overnight temperature for downy woodpeckers and, to a

lesser extent, white-breasted nuthatches. Furthermore, response to overnight temperature was highly variable between individuals within species (Supplementary Materials). We also showed that a pair of birds were more likely to be synchronized in their changes in morning foraging activity (i.e., higher correlation in their feeder activity profiles) when they flocked together more often over the course of the season, and this was not driven simply by spatial overlap (i.e., overlap in use of particular bird feeders). When examined together in the same model, the foraging activity of social partners appeared to have a greater effect than overnight temperature alone. However, the two effects cannot be neatly separated because all individuals in the population experienced similar overnight temperatures. Nevertheless, our analyses showed a clear effect of social partners even after accounting for overnight temperature, suggesting that individual environmental responses may be explained by the joint effects of individual foraging requirements and social connections (Table 2; Firth et al. 2015).

Our social network analyses of both downy woodpeckers and white-breasted nuthatches also point to winter social systems composed of a mix of some close male–female relationships and some diffuse associations in conspecific flocks. While we were not able to identify mating and kin relationships in this population, our results support the findings of prior studies showing some level of year-round territories in both species (Matthysen 1993; Matthysen et al. 1993). However, our results also indicate that there are individuals that maintain more diffuse associations with multiple individuals in the population. We were not able to determine whether these individuals are offspring, dispersers, floaters, or other winter residents in the population. In addition, white-breasted nuthatches and downy woodpeckers participate in mixed-species flocks in the winter at our study site. It is possible that the more diffuse associations between individuals in our population occurred as a result of the participation of individuals in mixed-species flocks. The presence of parids, such as the black-capped chickadee, increases the likelihood that white-breasted nuthatches and downy woodpeckers associate with one another (Dolby and Grubb 1999) and decreases the occurrence of vigilance behaviors (Dolby and Grubb 1998). Furthermore, there is some evidence to suggest that occurrences of parid-led mixed-

species flocks increase in colder temperatures (Klein 1988). This suggests that in times of energetic hardship, participation in parid-led mixed-species flocks can lead to increased foraging efficiency. It is possible that the patterns we have found are driven to some extent by interspecific sociality in the form of mixed-species flocks as well as conspecific sociality. Additional study is warranted to understand the degree to which conspecific and heterospecific relationships interact with foraging activity in this system. Nevertheless, we can conclude that different levels of social relations have the potential to influence foraging behavior of individuals.

There are two alternative ways in which sociality and temperature response could interact to determine actual morning foraging patterns: (i) similarity in temperature response could lead to social connections (i.e., homophily due to physiology), or (ii) sociality could modulate foraging activity despite optimal behavior from an energetics perspective (**Figure 4**). These two alternatives could have very different implications for the effect of sociality on winter survival. For example, if the observed correlation between foraging activity and social networks is driven by homophily (similarity in temperature response), shared responses may drive social structure in wild

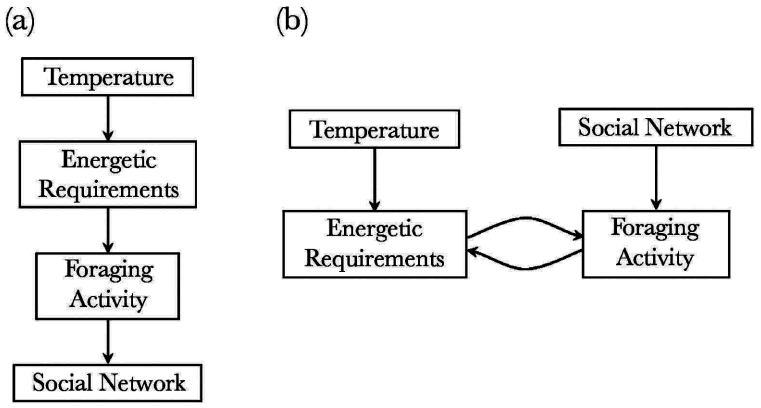

Figure 4 Two alternative hypotheses for the emergent relationship between temperature, foraging activity and social networks. In the first hypothesis (a), temperature regulates individual energetic needs, which affects foraging activity, while individuals with similar foraging activity patterns form social connections in the network. In the second hypothesis (b), foraging activities are affected by both energetic requirements and existing social connections. In turn, the social influence on foraging activity can cause mismatch between foraging behavior and optimal energetic regulation if social partners have different energetic requirements.

populations. Alternatively, if individual foraging activity is modulated by social partners, realized foraging patterns may sometimes be at odds with optimal responses to the environment. Such social effects on optimal foraging could have multiple causes. The learned benefits of social interactions, including higher foraging efficiency and higher consistency in foraging rate, may supersede optimal responses to temperature or other environmental conditions (Sullivan 1984; Hake and Ekman 1988). Similarly, carryover effects of social relations in other contexts, such as breeding pairs, parent–offspring relations, or participation in mixed-species flocks, may also lead individuals to adjust their foraging strategies to match their social partners, even when it is not individually optimal. This may especially be true in species like downy woodpeckers and white-breasted nuthatches that maintain year-round relations with mates. Socially driven foraging behavior may also be a product of foraging tradeoffs faced by individuals when balancing predation risk and energetics. For example, intraspecific competition or high variability in individual foraging abilities may result in an energetic mismatch for some individuals if collective foraging behavior restricts access to food or if individual foraging rates are highly variable (Ekman and Askenmo 1984). Whether or not such energetic mismatches within flocks could also ultimately sever or weaken connections and destabilize network structure is not yet known. However, there remains great potential for physiology and sociality to intersect in a variety of ways.

Our findings reinforce previous findings that some, though perhaps not all, small wintering bird species respond to low temperature by increasing foraging rates as predicted by theoretical models focusing on the effects of energy reserves (Evans 1969; Houston and McNamara 1993). For example, Bonter et al. (2013) used similar methods to study four species in Ithaca, NY and found that black-capped chickadees, tufted titmice, and whitebreasted nuthatches increased feeder visitations with decreases in average daily temperature, while house finches did not. In our study, we found that the relationship between overnight temperature and morning feeder visitations was weak for downy woodpeckers and even weaker for white-breasted nuthatches. There are multiple potential explanations for the discrepancies between theoretical predictions and the weak observed relationships between temperature and foraging rates. First, both species are known to roost

in tree cavities (Bent et al. 1948), and these roosts may dampen the variation in nightly temperatures experienced by the birds. Second, feeder visitation patterns for white-breasted nuthatches are likely affected by another component of foraging behavior that is difficult to capture in RFID studies: food caching. Decreasing temperature may prompt white-breasted nuthatches to gather more seeds from feeders for its cache in afternoons (Pravosudov and Grubb 1997, and suggested by results in Bonter et al. 2013, which is based on daily visits in response to daily temperatures). As a result, morning feeder visitations may not capture increased overall foraging rates if those birds spend more time retrieving caches after cold nights. Thus, it is important to consider that different foraging strategies and storage capabilities can result in slight differences in detection rates at feeders and different apparent foraging patterns for each species.

Future Directions

Our study opens the door to new questions about the drivers of foraging behavior of small birds that winter in temperate regions. Do foraging similarities regulate sociality, or does sociality influence foraging activity above and beyond individual optimal energy management? There are paths forward for experimental studies to explore the interplay between social networks and physiology in this context. For example, to understand the effects of overnight temperature on both fat reserves and foraging activity, RFID technology could be paired with controlled roost experiments to observe and/or manipulate the overnight temperatures individuals experience (e.g., Hatchwell et al. 2009). Manipulation of roosting temperature could potentially determine causality and help draw more direct interpretations about the effects of individual physiological variation (e.g., fat reserves) on social associations and vice versa. Furthermore, a study of the full annual cycle of the social systems at our study site is needed to clarify the degree to which breeding season social relations influence winter social relations in these species. It is also necessary to investigate interspecific social relations that occur during mixed-species foraging flocks to determine the extent of heterospecific influences on social and foraging behaviors. These birds have profoundly complex social

lives to navigate in addition to surviving harsh temperate winters. We suggest that further merging of concepts from classic foraging theory (e.g., Houston and McNamara 1993) and network theory would be productive to gain insights into how foraging birds balance environmental responses with social behaviors.

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